



## Invited research article

## Human footprint and climate disappearance in vulnerable ecoregions of protected areas

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## ABSTRACT

Ecoregions are distinct groups of natural communities and species. Currently, some ecoregions of the world are considered as vulnerable. Protected areas (PAs) can support the conservation of such vulnerable ecoregions. In this study, global PAs in different International Union for the Conservation of Nature (IUCN) management categories and their vulnerable ecoregions were studied, and human footprint and climate disappearance were assessed. The human footprint was found to drive the ecoregional vulnerability of PAs, which was high for vulnerable ecoregions in Europe, North America, and in smaller regions of Asia, Australia, New Zealand, and South America. These PAs included different biomes (excluding montane grasslands and shrublands) and affected IUCN PA management categories. Discrepancies may exist between observations and the present assignment of PAs to IUCN categories considering the extent of the human footprint; hence, these categories need to be re-evaluated based on human influence. The obtained results indicate that vulnerable ecoregions in forest, tundra, and mangrove biomes in PAs of eastern North America, Europe, south-eastern Asia, Australia, New Zealand, and the Pacific islands face high risks from climate disappearance. The ecoregional vulnerability of PAs to both human influence and climate change was high in temperate broadleaf and mixed forests in south-eastern Asia, Europe, Australia, and New Zealand. For global PAs, we propose that: 1) long-term monitoring should be conducted for changes in temperature and precipitation in vulnerable ecoregions such as forest, tundra, and mangrove biomes; and 2) human influence and climate change are integrated into adaptive strategies for the conservation of vulnerable PA ecoregions.

## 1. Introduction

Because of their characteristic, geographically distinct assemblages of natural communities and species, ecoregions have been identified as priorities for conservation by the World Wildlife Fund (WWF), and are globally conserved as protected areas (PAs; Olson et al., 2001). Both the number and size of PAs have been increasing rapidly over the past 20 years, with the aim of protecting 13–17% of the world's land surface by 2020 (according to Aichi Biodiversity Targets to 2020, <https://www.cbd.int/sp/targets/>) and thus, preventing the further loss of threatened species (Waldron et al., 2013; Watson et al., 2014; Venter et al., 2014). A global PA network can strongly contribute to the conservation of ecoregions. PA monitoring networks, databases, and evaluation systems have been developed to conserve ecoregions ranging from regional to global scales (Hoekstra et al., 2005; Jenkins and Joppa, 2009; Barr et al., 2011; Venter et al., 2014). For example, based on various aims

and concerns, the International Union for the Conservation of Nature (IUCN) developed management categories for global PAs, which have been applied in ecoregion conservation (<https://www.iucn.org/>). The World Database on Protected Areas (WDPA, <http://www.wdpa.org/>) plays an important role in the evaluation of regional and global PAs, and performs gap analyses, based on the ecoregion concept (Maxted et al., 2008; Jenkins and Joppa, 2009; Barr et al., 2011; Venter et al., 2014; Dinerstein et al., 2017).

Anthropogenic impacts and rapid climate change have been reported to threaten the effectiveness of PAs with regard to ecoregion conservation (Wittemyer et al., 2008; Mawdsley et al., 2009; Araújo et al., 2011; Watson et al., 2014). Global human activities and agricultural growth may both decrease PA coverage and obstruct PA expansion (Wittemyer et al., 2008). Furthermore, population growth has increased on the edges of PAs across ecoregions, countries, and continents, which could exacerbate anthropogenic threats to biodiversity in

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PA buffer zones (McKinney, 2002; Wittemyer et al., 2008; Joppa et al., 2009). Human activities can drive alien species into PAs and affect wilderness quality, wildlife habitat, and biological systems (Pauchard and Alaback, 2004; Foxcroft et al., 2007; Barros and Pickering, 2014).

Past climate change can lead to variations in biodiversity distribution patterns, as well as in both the composition and function of ecosystems, and to regional and global extinction of biodiversity (Williams et al., 2007; Svenning et al., 2015; Weigelt et al., 2016). The climatic dissimilarity between past and modern climates may result in the lack of a modern analogue for past climates (i.e., climate disappearance), such that the development of species associations and biomes has no modern counterpart (Williams et al., 2007; Svenning et al., 2015; Weigelt et al., 2016). As a consequence, climate disappearance can lead to species loss and extinction (Williams et al., 2007). Key risks are associated with future climate states without current analogue, due to increasing cumulative concentrations and emissions of carbon dioxide. Climate disappearance may also lead to similar extinction dynamics in the future (Williams et al., 2007; Pacifici et al., 2015). Beaumont et al. (2011) have reported that the ecoregions of tropical montane regions and of the poleward portions of continents would be threatened by climate disappearance. In addition, in recent centuries, past climate change and human activities interacted and played an important role in affecting the effectiveness of PAs for biodiversity conservation (Leu et al., 2008; Mawdsley et al., 2009; Porter et al., 2013). Hence, anthropogenic climate change has been shown to weaken the ability of PAs to protect ecoregions (Mawdsley et al., 2009; Araújo et al., 2011). For example, human-induced climate change may threaten regional PAs and lead to the loss of conservation functions (Hannah, 2008). Therefore, globally, many ecoregions in PAs are vulnerable due to anthropogenic impacts and rapid climate change.

The assessment of existing PAs is an important stage in systematic conservation planning (Margules and Pressey, 2000). For example, Barr et al. (2011) developed an effective measure for the determination of global PA coverage for ecoregions, and evaluated the ability of these PAs to protect ecoregions across different countries. Furthermore, global PAs under management categories I–IV contribute to biodiversity conservation; however, there are still vulnerabilities and gaps in the global plant protection that need to be overcome to meet the Convention on Biological Diversity's protection targets (Jenkins and Joppa, 2009; Barr et al., 2011; Venter et al., 2017). To assess the effectiveness of PAs, indicators of threats to ecoregions need to be identified and effective methods for the conservation of biodiversity need to be proposed (Hoekstra et al., 2005; Barr et al., 2011).

Recent studies across different regions have reported the negative effects of anthropogenic activities and of climate disappearance on threatened species and ecosystem stability (Beaumont et al., 2011; Dinerstein et al., 2017). The human footprint is a tool for conservation planning at the ecoregional scale, which quantifies a continuum of anthropogenic impacts on terrestrial ecosystems and identifies the remaining large global wild areas (Sanderson et al., 2002; Woolmer et al., 2008). Previous studies have demonstrated that the human footprint is significantly related to ecoregional biodiversity (Leu et al., 2008; Woolmer et al., 2008; Etter et al., 2011). The quantification of climate disappearance between current and future states is an effective method for the evaluation of risks of species loss and extinction in response to future climate change (Williams et al., 2007; Beaumont et al., 2011; Watson et al., 2013; Bellard et al., 2014). Watson et al. (2013) defined a measure of similarity between the expected future climate of a region and its present state for the assessment of ecoregional vulnerability, and proposed recommendations for the adaptation of the conservation of ecoregion biodiversity and ecosystems. If anthropogenic disturbance and disappearing climates are considered interactively, their impacts and threats/risks to PAs are close to reality. Climate change is causing global warming due to anthropogenic activities in the past 50 years, and the similar changing trends would continue in the future (Porter et al., 2013; Jones et al., 2016; <http://www.ipcc.ch>). Such anthropogenic

climate change may drive biodiversity loss, and decrease conservation functions of PAs (Keppel et al., 2012; Porter et al., 2013; Svenning et al., 2015). Maps of future climate change can be projected based on the assessment of concentrations of anthropogenic greenhouse gases and other pollutants (<http://www.ccafs-climate.org>). Hence, it is possible to assess effects of future climate change on vulnerable ecoregions of PAs in the consideration of human disturbance. Although the assessments of eco-vulnerability using disappearing climates may have limitations, similar approaches have been widely used for conservation planning with a focus on global ecoregions (Williams et al., 2007; Beaumont et al., 2011; Watson et al., 2013; Pacifici et al., 2015).

Here, both the human footprint and climate disappearance were used as indicators of threats to ecoregions, and assessed their potential global impacts on vulnerable PA ecoregions. PA data was collected from the WDPA based on IUCN protected area management categories (<http://www.wdpa.org/>), ecoregion data from Olson et al. (2001), and human footprint data from Sanderson et al. (2002). Then, human footprint indices and degrees of disappearance of future PA climates were calculated through an extensive, global PAs sample. Finally, vulnerable PA ecoregions were identified according to high human footprint and climate disappearance, and several effective conservation management methods for global biodiversity were proposed.

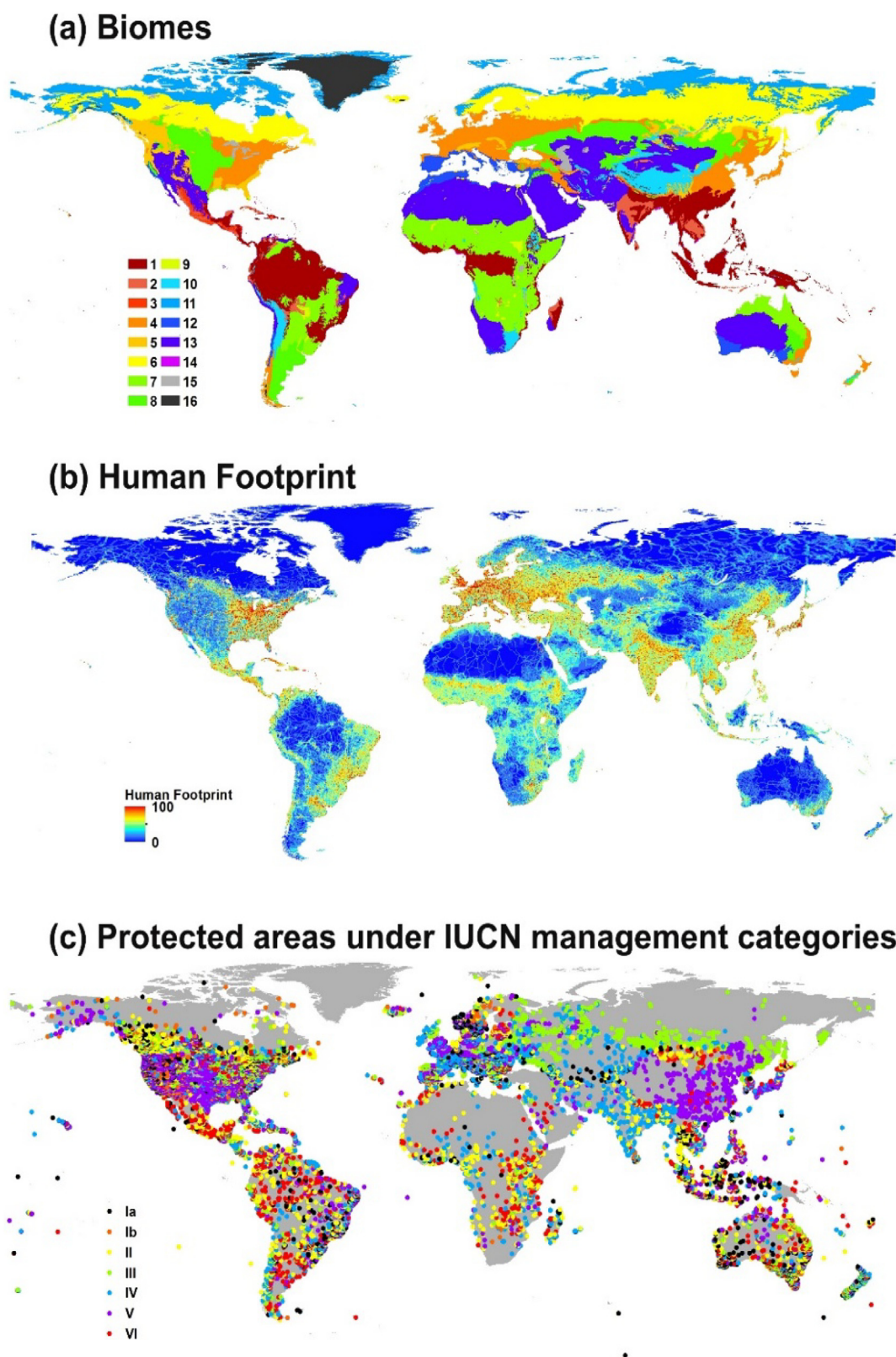
## 2. Materials and methods

### 2.1. Protected areas (PAs)

PA data with polygons and points were obtained from the UNEP-WCMC WDPA (<http://www.wdpa.org/>; accessed in July 2017). In total, 234,008 PA records, comprising 215,427 polygons and 18,581 points, were released by the WDPA in July 2017, covering 245 countries and territories. Where boundary data was unavailable for point data, both the latitude and longitude of the centermost point were requested as a reference point for the PA (<http://www.wdpa.org/>). ArcGIS 10.2 (Esri, Redlands, CA, USA) was used to convert polygons into point data based on the latitude and longitude of the centermost points, creating point data for 234,008 PAs for further study. PAs in IUCN management categories I–VI were selected as study cases; the management categories are as follows: 1) Ia. Strict Nature Reserve; 2) Ib. Wilderness Area; 3) II. National Park; 4) III. Natural Monument or Feature; 5) IV. Habitat/Species Management Area; 6) V. Protected Land/Seascape; 7) VI. Protected area with sustainable natural resource use (<https://www.iucn.org/>). These categories are based on the management objectives of the PAs with regard to human activity and land use (Leroux et al., 2010). The present assignment of protected areas to IUCN categories corresponds to the expected extent of anthropogenic impacts on both biodiversity and species (Dudley, 2008; Leroux et al., 2010).

### 2.2. Ecoregions

Ecoregions are units for conservation action across different spatial scales (Olson et al., 2001). The WWF has delineated 825 terrestrial ecoregions globally, in 14 major biomes (see Fig. 1a), and three conservation statuses have been applied (i.e., “critical or endangered”, “vulnerable”, and “relatively stable or intact”; <https://www.worldwildlife.org/>). The study of Olson and Dinerstein (1998) provided an effective approach for the assessment of the vulnerability of global ecoregions. Vulnerable ecoregions (i.e., “critical or endangered” and “vulnerable”) are threatened by total habitat loss, degree of fragmentation, poor water quality, and estimates of future threat. The habitats, biodiversity, and ecosystems of non-vulnerable ecoregions are relatively stable or intact (Olson and Dinerstein, 1998). The details of the vulnerability assessment approach have been reported in the study of Olson and Dinerstein (1998). Here, “critical or endangered” and “vulnerable” ecoregions have been regarded as vulnerable, and “relatively stable or intact” ecoregions as non-vulnerable.



**Fig. 1.** Maps of (a) biomes; (b) human footprint; and (c) protected areas. Codes for biomes: 1 - Tropical and Subtropical Moist Broadleaf Forests; 2 - Tropical and Subtropical Dry Broadleaf Forests; 3 - Tropical and Subtropical Coniferous Forests; 4 - Temperate Broadleaf and Mixed Forests; 5 - Temperate Conifer Forests; 6 - Boreal Forests/Taiga; 7 - Tropical and Subtropical Grasslands, Savannas, and Shrublands; 8 - Temperate Grasslands, Savannas, and Shrublands; 9 - Flooded Grasslands and Savannas; 10 - Montane Grasslands and Shrublands; 11 - Tundra; 12 - Mediterranean Forests, Woodlands, and Scrub; 13 - Deserts and Xeric Shrublands; 14 - Mangroves; 15 - Inland Water; 16 - Rock and Ice. Codes for IUCN categories: Ia - Strict Nature Reserve; Ib - Wilderness Area; II - National Park; III - Natural Monument or Feature; IV - Habitat/Species Management Area; V - Protected Landscape/Seascape; VI - Protected Area with sustainable natural resource use.



The intersection function of ArcGIS 10.2 (Esri, Redlands, CA, USA) can calculate the overlap between two groups of data, allowing the identification of similar features. This function was used to assess the vulnerability of ecoregions (i.e., vulnerable and non-vulnerable PA ecoregions). Thus, data was obtained for the vulnerability of central PA ecoregions.

### 2.3. Quantifying human footprint in vulnerable PA ecoregions

Sanderson et al. (2002) created a map of the Human Influence Index (HII), reported at a spatial resolution of 1 km<sup>2</sup>, based on human population pressure (population density), land use and infrastructure (built-up areas, night-time lighting, and land use/cover), as well as access (coastlines, roads, railroads, and navigable rivers). Human footprint is strictly related to HII; a high human footprint index indicates the intactness, naturalness, and function of natural communities. Based on the above-mentioned map of human influence, we calculated human footprint (HF) using the following equation (Sanderson et al., 2002; Leroux et al., 2010):

$$HF_i = \frac{(HII_i - HII_{\min,j}) \times 100}{HII_{\max,j} - HII_{\min,j}}$$

where  $i$  represents the cell and  $j$  represents the sub-region of which the cell is a member. Ecological sub-regions indicate the primary spatial variation in dominant biological communities within an ecoregion (Sanderson et al., 2002; Woolmer et al., 2008).

The human footprint index ranges from 1 to 100 (see Fig. 1b). Based on Woolmer et al. (2008), human footprint indices were classified into three levels to quantify the degree of anthropogenic effects. Indices from 20 to 40 indicated a high human footprint for vulnerable PA ecoregions, while indices above 40 indicated an extremely high human footprint.

Previous studies have shown that human footprint negatively affects biodiversity (Kier et al., 2005a, 2005b; Venter et al., 2016). Here, PA ecoregional vulnerability was used as a binary response variable (vulnerable as 1, and non-vulnerable as 0), and the human footprint index was used as the explanatory variable, based on point data. Then, data was removed that had the same human footprint index, type of ecoregion, IUCN category, and ecoregional vulnerability. The final number of sampled PA ecoregions was 17,051 (see Fig. 1c). A General Linear Model (GLM) was used to test the relationship between the human footprint (the explanatory variable) and PA ecoregional vulnerability (the response variable) across 14 major biomes and IUCN categories I–VI.

The average human footprint of vulnerable PA ecoregions was computed, across different biomes and IUCN categories, to identify vulnerable PA ecoregions with high human footprint, based on Woolmer et al. (2008). The IUCN guide of PAs identifies common goals across all IUCN categories, including the conservation of genetic, species, community, ecosystem, and landscape diversity, as well as the processes that link these different elements (Dudley, 2008). The qualitative goal of the IUCN toward nature conservation can be expressed by a gradient of naturalness among PA categories (i.e., Ia = Ib > II = III > IV = VI > V, from the most natural to the least natural; see Dudley, 2008; Leroux et al., 2010). Both ecosystem structure and human activity define naturalness in PAs (IUCN, 1994). Based on the studies of Dudley (2008) and Leroux et al. (2010), human footprint was used as a reasonable global proxy of naturalness with which to assess the potential vulnerability of ecoregions in PAs across different IUCN categories, considering human influences on PAs. An independent-sample  $t$ -test was performed to test the differences between the human footprint affecting vulnerable ecoregions across IUCN categories, which was used to map vulnerable PA ecoregions with extremely high human footprint.

### 2.4. Quantifying climate disappearance in vulnerable PA ecoregions

First, eight climate variables were used (obtained from the WorldClim database at 5.0-min resolution; Hijmans et al., 2005; [www.worldclim.org](http://www.worldclim.org)) to analyze the dissimilarity between current and future climates (Williams et al., 2007; Bellard et al., 2014). These variables provide a combination of means, extremes, and seasonality that influence the distribution and physiology of plant species, and were as follows: 1) annual mean temperature (°C), 2) temperature seasonality (standard deviation\*100), 3) max temperature of the warmest month (°C), 4) min temperature of the coldest month (°C), 5) annual precipitation (mm), 6) precipitation of the wettest month (mm), 7) precipitation of the driest month (mm), and 8) precipitation seasonality (coefficient of variation, <http://www.worldclim.org/>). The current climatic variables covered the period 1950–2000 (Hijmans et al., 2005). Two greenhouse gas concentration scenarios were used (i.e., Representative Concentration Pathways (RCPs) 4.5 and 8.5) from average maps of three global climate models (ccma\_canesm2, csiro\_mk3, and mohc\_hadgem2) set in the 2080s (2071–2099; <http://www.ccafs-climate.org>). RCP 4.5 differs from RCP 8.5 in that RCP 8.5 has larger cumulative concentrations and emissions of carbon dioxide. Consequently, it predicts a different climatic scenario based on different concentrations of anthropogenic greenhouse gases and other pollutants. RCP 8.5 and RCP 4.5 represented high and low concentration scenarios, respectively (<http://www.ipcc.ch/>).

Current and future climates were first extracted based on the point data of 17,051 PAs. Based on the study of Bellard et al. (2014), PAs were assumed to have specific climates that explain the biodiversity found in conservation areas. Historical processes, contemporary ecological factors, inherent biological properties of taxa, topography, soil types, and their combinations can all contribute to the high rates of endemism in these PAs. To determine the dissimilarity between current and future climates within PA ecoregions, these ecoregions were assumed to have specific climates that explain their biodiversity. Based on this assumption, the methodology developed by Williams et al. (2007) was used to quantify climatic dissimilarity between current and future states within each PA ecoregion. The following assessment of the Standardized Euclidean Distance (SED) was used:

$$SED_j = \sqrt{\sum_{k=1}^8 \frac{(a_k - b_k)^2}{S_k^2}},$$

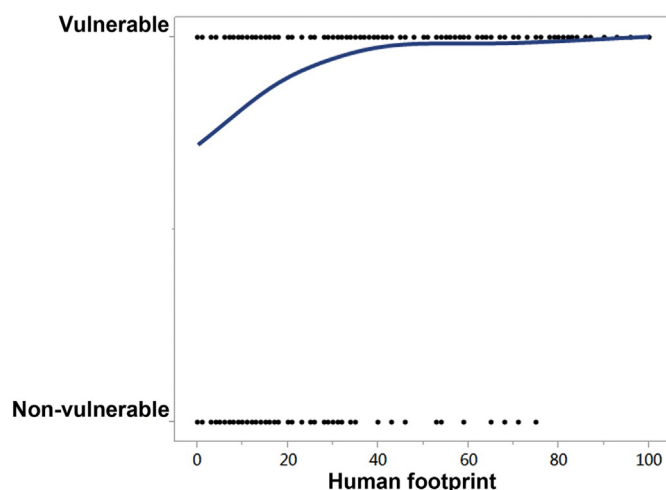
where  $a_k$  and  $b_k$  represent the current and future (2080s) climate variables  $k$  in PA  $j$ , and  $S_k$  represents the standard deviation of the intra-annual variability for the current climate period (1950–2000), which covers the metrics of seasonality for temperature and precipitation.

Based on Williams et al. (2007), the average climatic dissimilarity between current and future states across all PA ecoregions was used as the threshold of disappearing climate for low and high concentration scenarios. The details of this method can be found in Williams et al. (2007). The threshold of climate disappearance was 4.641 for the low concentration scenario and 5.827 for the high concentration scenario. Finally, the average number of disappearing climates in vulnerable PA ecoregions was calculated for each biome in both low and high concentration scenarios. This was used a linear regression model to explore their relationships. If the disappearing climates of biomes exceeded the threshold values, there was a high risk of climates disappearing in vulnerable PA ecoregions (Williams et al., 2007; Bellard et al., 2014).

## 3. Results

### 3.1. Human footprint

The human footprint was significantly related to PA ecoregional vulnerability; the number of PAs with a human footprint above 20 exceeded largely those with a human footprint below 20 ( $P < 0.05$ , see



**Fig. 2.** Relationship between human footprint and PA ecoregional vulnerability. The blue line represents the positive relationship between human footprint and PA ecoregional vulnerability based on GLM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Human footprint in non-vulnerable and vulnerable protected area ecoregions, based on biomes and IUCN categories.

	Non-vulnerable		Vulnerable		P-values
	Mean	SD	Mean	SD	
Biome					
1	17.7	14.1	32.1	20.0	< 0.001
2	No data	No data	34.1	20.5	
3	No data	No data	31.6	18.7	
4	24.2	19.8	41.6	23.2	< 0.001
5	28.0	22.8	32.1	22.6	0.0034
6	24.7	23.1	29.4	24.1	0.0103
7	19.5	16.5	23.6	18.3	0.0259
8	31.6	21.3	36.3	23.1	0.2709
9	19.5	9.5	39.2	24.0	0.0021
10	19.1	13.5	19.7	10.6	0.6964
11	6.2	7.7	22.6	19.1	< 0.001
12	No data	No data	36.6	22.6	
13	24.5	21.5	27.4	20.6	0.0345
14	36.5	25.2	28.6	21.5	0.0435
IUCN protected area management category					
Ia	15.3	14.4	30.1	21.4	< 0.001
Ib	11.8	10.4	22.5	19.4	< 0.001
II	15.5	13.3	26.6	19.1	< 0.001
III	25.6	21.4	39.5	23.4	< 0.001
IV	21.4	18.9	37.8	22.8	< 0.001
V	31.5	23.2	40.5	23.4	< 0.001
VI	17.7	14.7	31.2	20.4	< 0.001

We tested (*P*-values) the relationship between human footprints and ecoregional vulnerability of protected areas in 14 major biomes and IUCN categories I–VI. Codes for biomes: 1 - Tropical and Subtropical Moist Broadleaf Forests; 2 - Tropical and Subtropical Dry Broadleaf Forests; 3 - Tropical and Subtropical Coniferous Forests; 4 - Temperate Broadleaf and Mixed Forests; 5 - Temperate Conifer Forests; 6 - Boreal Forests/Taiga; 7 - Tropical and Subtropical Grasslands, Savannas, and Shrublands; 8 - Temperate Grasslands, Savannas, and Shrublands; 9 - Flooded Grasslands and Savannas; 10 - Montane Grasslands and Shrublands; 11 - Tundra; 12 - Mediterranean Forests, Woodlands, and Scrub; 13 - Deserts and Xeric Shrublands; 14 - Mangroves. Codes for IUCN categories: Ia - Strict Nature Reserve; Ib - Wilderness Area; II - National Park; III - Natural Monument or Feature; IV - Habitat/Species Management Area; V - Protected Landscape/Seascape; VI - Protected Area with sustainable natural resource use.

**Fig. 2).** This relationship was positive in all 14 biomes except for montane grassland and shrubland and temperate grasslands, savannas, and shrublands (no significance,  $P > 0.05$ ), and mangrove (significant negative relationship,  $P < 0.05$ ) ecoregions (see [Table 1](#)). The human footprint index exceeded 20 across vulnerable PA ecoregions belonging to 13 biomes, excluding montane grasslands and shrublands. The human footprint of vulnerable ecoregions was highest in temperate broadleaf and mixed forests (41.6), and lowest in tundra (22.6, see [Table 1](#)).

A significant positive relationship was identified between the human footprint and PA ecoregional vulnerability based on IUCN categories ( $P < 0.001$ ), while significant differences in human footprint were found between PA ecoregions across IUCN categories ( $P < 0.05$ ). The human footprint was high across different IUCN categories ( $> 20$ ); it was highest in Protected Landscape/Seascape, and lowest in Wilderness Area. The human footprint of Strict Nature Reserve was significantly higher than that of Wilderness Area and National Park ( $P < 0.05$ , see [Table 1](#)).

Vulnerable PA ecoregions with high human footprint indices ( $> 40$ ) were mainly distributed across Europe, North America, and parts of Asia, Australia, New Zealand, and South America. These areas contain many vulnerable PA ecoregions with high human footprint indices, excluding Wilderness Area (see [Fig. 3](#)). Vulnerable habitat/species management area ecoregions with high human footprints were localized in South Asia, and vulnerable protected landscape/seascape ecoregions were found in China (see [Fig. 3](#)).

### 3.2. Disappearing climates

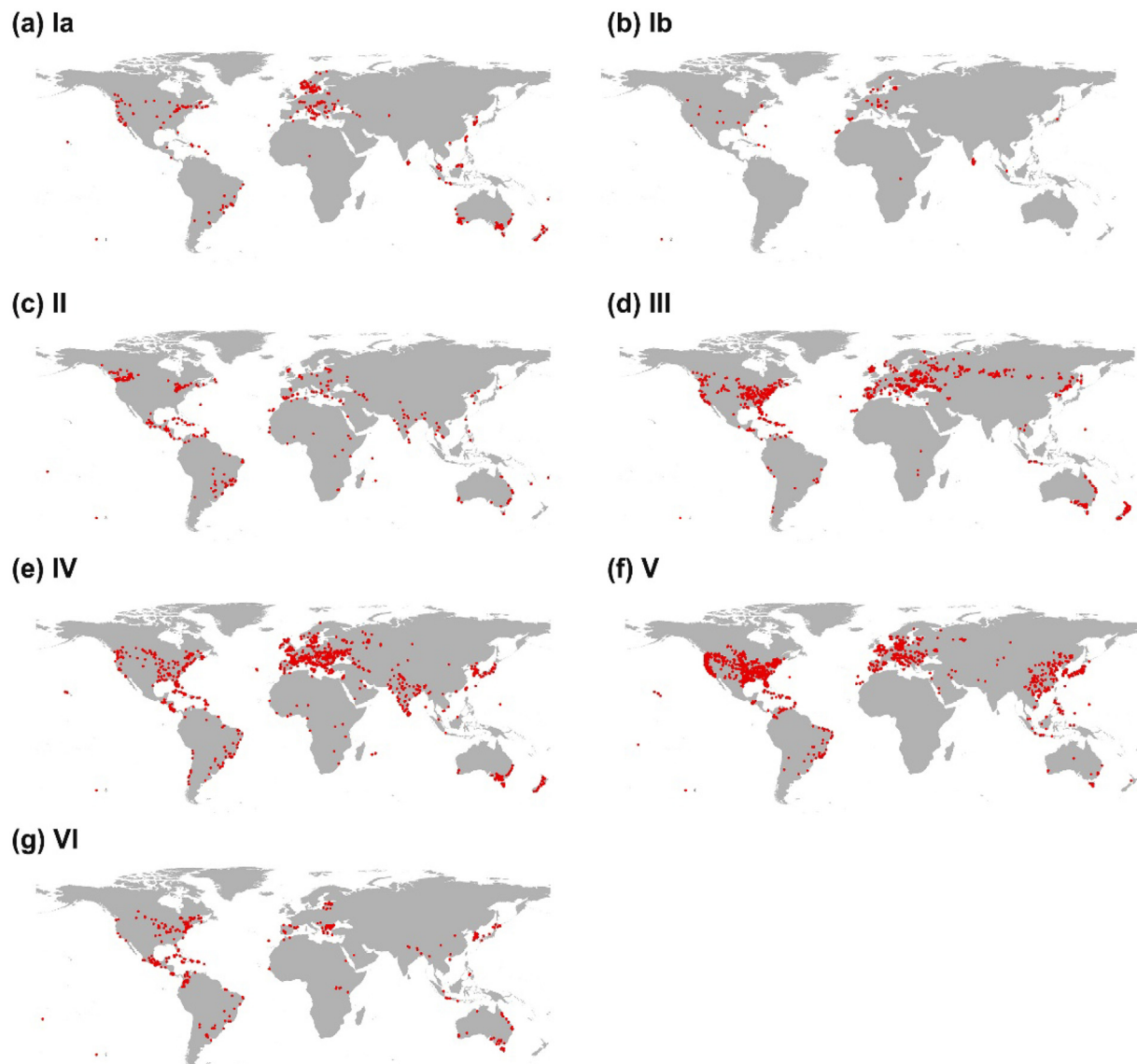
There was a significant relationship between the climatic dissimilarity of vulnerable PA ecoregions in both low and high CO<sub>2</sub> concentration scenarios (Slope = 0.978–1.057,  $R^2 > 0.850$ ,  $P < 0.001$  for all 14 biomes, see [Table 2](#)). Climate disappearance of vulnerable PA ecoregions in the low concentration scenario was consistent with that of the high concentration scenario (see [Table 2](#)). Vulnerable ecoregions, including tropical and subtropical moist broadleaf, dry broadleaf, and coniferous forests, temperate broadleaf and mixed forests, boreal forests and taiga, as well as tundra and mangroves face high risks of disappearing climates (see [Table 2](#)). These vulnerable ecoregions are distributed throughout the eastern regions of North America, Europe, south-eastern Asia, Australia, New Zealand, and the Pacific islands (see [Fig. 4](#)).

## 4. Discussion

This study quantified the human footprint and climate disappearance in vulnerable PA ecoregions based on 17,051 global PAs. Human influence and climate change are the main drivers for the current global biodiversity loss, and the establishment of PAs is one of the most effective biodiversity conservation approaches ([Margules and Pressey, 2000](#); [Wade et al., 2003](#); [Venter et al., 2016](#); [Dinerstein et al., 2017](#)). Effectiveness of PAs may decrease due to high human footprints and high risk of climate disappearance in ecoregions of forest, tundra, and mangrove. We need to regard vulnerable ecoregions of PAs belonging to temperate broadleaf and mixed forests as key conservation and monitoring areas because both human footprint and disappearing climates would exist at extremely high levels (see [Tables 1 and 2](#)). This study, therefore, could help to formulate feasible methods for conservation management of PAs.

### 4.1. Human footprint in vulnerable ecoregions of PAs

A significant positive relationship was found between human footprints and PA ecoregional vulnerability in all 14 biomes except for montane grasslands and shrublands, temperate grasslands, savannas, and shrublands and mangroves. This result suggests that the human



**Fig. 3.** Distribution of vulnerable PA ecoregions with extremely high human footprint. Codes for IUCN categories: Ia – Strict Nature Reserve; Ib – Wilderness Area; II – National Park; III – Natural Monument or Feature; IV – Habitat/Species Management Area; V – Protected Landscape/Seascape; VI – Protected Area with sustainable natural resource use.

footprint is a good indicator for vulnerable PA ecoregions. Human footprint can either directly or indirectly affect biodiversity and ecosystems by actions that induce land cover change and lead to ecosystem degradation (Woolmer et al., 2008; Leroux et al., 2010). A precise determination of the extent of the human footprint is essential for an improvement of the management efficiency of biodiversity and ecosystems in ecoregions (Woolmer et al., 2008; McShane et al., 2011).

The human footprint of vulnerable PA ecoregions in several biomes (excluding montane grasslands and shrublands) was high in Europe, North America, and in areas of Asia, Australia, New Zealand, and South America (Sanderson et al., 2002; Woolmer et al., 2008). Numerous studies have quantified species diversity across different ecoregions and used biogeographic units at ecoregional scale to protect a full range of representative areas (Olson et al., 2001; Woolmer et al., 2008; Dinerstein et al., 2017). For example, Kier et al. (2005a, 2005b) described the global plant diversity of ecoregions and guided conservation efforts based on human influence. PAs cover and protect large areas of ecoregions across different biomes; however, large overlaps may exist between areas with high human footprint and vulnerable PA ecoregions (Kier et al., 2005a, 2005b; Woolmer et al., 2008; Venter et al., 2016;

Dinerstein et al., 2017).

This study found that the human footprint was high in global temperate broadleaf and mixed forests, which have rich forest resources, and are threatened by human influences. Wade et al. (2003) demonstrated that > 50% of temperate broadleaf and mixed forest biomes have been fragmented or removed by humans, a result that is partially consistent with the findings of our study. Although the role of PAs is to prevent the human population from expanding into vulnerable ecoregions, inconsistent conservation management practices have nevertheless caused persistent human impact (McShane et al., 2011). For example, visitors in or around PAs may exacerbate human pressures on ecoregions (Buckley et al., 2017). Furthermore, several biome ecosystems (e.g., tundra) are unstable, and both habitat fragmentation and biological invasions caused by human activities increases the risk of biodiversity loss and species extinction in PAs (Pauchard and Alaback, 2004; Foxcroft et al., 2007; Barros and Pickering, 2014; McConnachie et al., 2015). Therefore, it is important to propose different PA management strategies for the conservation of vulnerable ecoregions across a variety of biomes.

The IUCN developed protected area management categories for

**Table 2**  
Disappearing climate assessment of vulnerable PA ecoregions across 14 biomes.

Biome	Low concentration		High concentration		Slope	$R^2$	$P$ -values
	Mean	SD	Mean	SD			
1	<b>7.928</b>	<b>20.655</b>	<b>10.177</b>	<b>20.837</b>	0.998	0.978	< 0.001
2	<b>4.772</b>	<b>9.180</b>	<b>6.210</b>	<b>9.146</b>	0.983	0.973	< 0.001
3	<b>4.979</b>	<b>19.610</b>	<b>6.151</b>	<b>19.494</b>	0.992	0.997	< 0.001
4	<b>6.003</b>	<b>10.802</b>	<b>7.171</b>	<b>10.946</b>	1.000	0.974	< 0.001
5	3.089	5.082	3.771	5.353	1.027	0.951	< 0.001
6	<b>5.246</b>	<b>11.206</b>	<b>6.722</b>	<b>11.606</b>	1.022	0.974	< 0.001
7	2.962	5.472	4.003	6.128	1.085	0.939	< 0.001
8	2.153	4.660	2.739	5.013	1.057	0.966	< 0.001
9	2.618	5.753	3.633	5.752	0.987	0.975	< 0.001
10	1.323	1.393	1.850	1.830	1.214	0.855	< 0.001
11	<b>5.471</b>	<b>9.332</b>	<b>7.107</b>	<b>9.159</b>	0.978	0.992	< 0.001
12	2.109	4.306	2.919	4.302	0.986	0.973	< 0.001
13	1.659	4.921	2.311	5.030	1.005	0.967	< 0.001
14	<b>7.078</b>	<b>14.900</b>	<b>8.645</b>	<b>14.760</b>	0.982	0.983	< 0.001

The bold values represent high risk of disappearing climates based on biomes. We tested (Slope,  $R^2$  and  $P$ -values) the relationships between disappearing climates in PA ecoregions in low and high concentration scenarios for each biome. Codes for biomes: 1 - Tropical and Subtropical Moist Broadleaf Forests; 2 - Tropical and Subtropical Dry Broadleaf Forests; 3 - Tropical and Subtropical Coniferous Forests; 4 - Temperate Broadleaf and Mixed Forests; 5 - Temperate Conifer Forests; 6 - Boreal Forests/Taiga; 7 - Tropical and Subtropical Grasslands, Savannas, and Shrublands; 8 - Temperate Grasslands, Savannas, and Shrublands; 9 - Flooded Grasslands and Savannas; 10 - Montane Grasslands and Shrublands; 11 - Tundra; 12 - Mediterranean Forests, Woodlands, and Scrub; 13 - Deserts and Xeric Shrublands; 14 - Mangroves.

global PAs, which have been globally accepted by national governments and international bodies (Leroux et al., 2010). However, discrepancies may exist between observations and the present assignment of PAs to IUCN categories, based on human activities and land use (Dudley et al., 2010; Leroux et al., 2010). The IUCN proposed the following order of categories based on human footprint size: Ia = Ib < II = III < IV = VI < V (Dudley, 2008). The results of this study indicate that the human footprint was high across all IUCN categories and the human footprint observed in vulnerable PA ecoregions was not consistent with this ranking. This suggests that conservation management needs to be adjusted based on the human footprint in PAs, otherwise the conservation efficiency weakens. The human footprint of the Strict Nature Reserve was significantly higher than that of the Wilderness Area and the National Park (Locke and Dearden, 2005; Dudley et al., 2010; Leroux et al., 2010). If human impact on Strict Nature Reserve ecoregions are increasingly persistent in PAs, they could be categorized as Habitat/Species Management Area or Protected Landscape/Seascape (Leroux et al., 2010). For the current Strict Nature Reserves, we need to reduce human population size and intensive land

use inside or adjacent to PAs with relatively small human footprints. Furthermore, the IUCN management categories for the Strict Nature Reserve with extremely high human footprints (i.e., > 40) should be changed, so that they are regarded as a Habitat/Species Management Area and a Protected Landscape/Seascape.

Here, the ranges of vulnerable PA ecoregions were determined on a global scale, and we suggest to use Fig. 3 as a reference for conservation management. The intensity of human activities needs to be controlled in vulnerable Natural Monuments or Feature, Habitat/Species Management Area, and Protected Landscape/Seascape ecoregions. The PAs that belong to these three IUCN categories require the protection of natural resources and of species diversity, as well as the sustainable production and provision of ecosystem services (Leroux et al., 2010). A high human footprint may break the balance between conservation and sustainable production of natural resources (Berlik et al., 2002; Gagné et al., 2015; Venter et al., 2016). For example, global and regional urbanization can result in the loss of Natural Monument or Feature, Habitat/Species Management Area, and Protected Landscape/Seascape ecoregions (Su et al., 2014; Doxa et al., 2017; Wood et al., 2017). Thus, losing conservation functions is a high risk for PAs.

#### 4.2. Disappearing climates in vulnerable PA ecoregions

The presented results suggest that forest, tundra, and mangrove biomes in eastern North America, Europe, south-eastern Asia, Australia, New Zealand, and the Pacific islands are threatened by climate change. These results are basically consistent with previous reports (Feeley and Silman, 2010; Beaumont et al., 2011; Watson et al., 2013; Bellard et al., 2014). Forests provide habitats for organisms, have a large carbon pool, and a high net primary productivity (Dixon et al., 1994; Gower et al., 2001; Pan et al., 2011). However, future changes in temperature and precipitation potentially affect biodiversity and ecosystems in forest ecoregions, as they can result in higher vapor pressure deficits and evaporation, thus reducing the availability of water for plant growth (Lindenmayer et al., 2006; Clark et al., 2011). Disappearing climates can threaten temperate broadleaf and mixed forests by seasonal changes involving periods of growth and dormancy (Gilliam, 2016). As a result, the community composition would change, and the loss of species diversity would potentially occur in temperate broadleaf and mixed forest PAs (Barbier et al., 2008; Gilliam, 2016). Net ecosystem production of temperate broadleaf and mixed forests may be vulnerable due to disappearing climates in PAs (Fernández-Martínez et al., 2016; Yuan et al., 2017). Furthermore, increasing temperatures can decrease the habitable areas for forest ecoregions, particularly in tropical biomes (Feeley and Silman, 2010; Clark et al., 2011; Wan et al., 2018). Although PAs can support the global conservation of vulnerable ecoregions, the negative effects of climate change will still impact forest ecoregions.



**Fig. 4.** Risk of climate disappearance in vulnerable PA ecoregions in the low concentration scenario.



Tundra ecoregions are primarily characterized by low temperatures; thus, higher temperatures would change their ecosystem structure, potentially making them more vulnerable to future climate change (Shaver et al., 1992; Olson et al., 2001). Myers-Smith et al. (2015) have shown that climate change explains shrub growth sensitivity across global tundra biomes. Global mangrove deforestation is occurring at a rate of 1–2% per year and extreme changes in monthly temperatures will place additional pressure on the resilience of mangroves in the future (Beaumont et al., 2011). Furthermore, climate change may drive invasive species into vulnerable ecoregions and PAs (Barros and Pickering, 2014; McConnachie et al., 2015). Biological invasions would reduce the species diversity in vulnerable PA ecoregions; therefore, considering climate change in the conservation of the natural integrity of PA ecoregions is urgent (Foxcroft et al., 2007; McConnachie et al., 2015).

Vulnerable PA ecoregions are rich in endemic species, have high taxonomic uniqueness, unique ecological or evolutionary phenomena, global rarity, and are representative for their biomes (Olson et al., 2001). Biological conservationists have proposed a variety of strategies for vulnerability assessment and conservation adaptation of vulnerable ecoregions in response to climate change (Mawdsley et al., 2009; Beaumont et al., 2011; Watson et al., 2013; Pacifici et al., 2015; Jones et al., 2016). We propose that: 1) long-term monitoring needs to be conducted for changes in temperature and precipitation in vulnerable forest, tundra, and mangrove biome ecoregions; and 2) both human footprint and climate change need to be integrated into PA conservation adaptation strategies (Olson et al., 2001; Watson et al., 2013).

Although this study tried to minimize the inherent uncertainties associated with an analysis on climate disappearance, not all possible uncertainties were taken into consideration. Attention was focused on the vulnerable ecoregions of PAs. Such an ecoregional vulnerability assessment was based on the approaches of Olson and Dinerstein (1998). Some ecoregions of PAs have become vulnerable in recent years and should be considered in future extreme drought scenarios. For example, climate disappearance may lead to loss of species from their current ranges and may fundamentally change the community composition of arid ecoregions of African PAs (Speranza et al., 2010; Thuiller et al., 2010). Furthermore, sufficient data needs to be obtained to quantify the threshold of biodiversity and ecosystem function loss due to disappearing climates. Finally, future studies need to focus more on the assessment of climate vulnerability of PAs across different spatial scales considering the interaction of human footprint and climate change.

## 5. Conclusions

We assessed human footprints and disappearing climates for vulnerable PA ecoregions, and identified those under high risk. We concluded that forest, tundra, and mangrove biome ecoregions (particularly, temperate broadleaf & mixed forests), and ecoregions in south-eastern Asia, Europe, Australia, and New Zealand are at risk owing to high human footprints and high risk of climate disappearance. There may be discrepancies between observations and the present assignment of PAs to IUCN categories, based on the assessment of human footprints. To improve management efficiency, we need to 1) change IUCN management categories for Strict Nature Reserve with extremely high human footprints; 2) conduct long-term monitoring for climate change in vulnerable forest, tundra, and mangrove PA ecoregions; and 3) integrate human footprints and climate change into conservation adaptation strategies for PA ecoregions.

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## References

- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. *Ecol. Lett.* 14, 484–492.
- Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. *Forest Ecol. Manag.* 254, 1–15.
- Barr, L.M., Pressey, R.L., Fuller, R.A., Segan, D.B., McDonald-Madden, E., Possingham, H.P., 2011. A new way to measure the world's protected area coverage. *PLoS One* 6, e24707.
- Barros, A., Pickering, C.M., 2014. Non-native plant invasion in relation to tourism use of Aconcagua Park, Argentina, the highest protected area in the Southern Hemisphere. *Mt. Res. Dev.* 34, 13–26.
- Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E., Yoccoz, N.G., Thuiller, W., 2011. Impacts of climate change on the world's most exceptional ecoregions. *Proc. Natl. Acad. Sci.* 108, 2306–2311.
- Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. *Glob. Ecol. Biogeogr.* 23, 1376–1386.
- Berlik, M.M., Kittredge, D.B., Foster, D.R., 2002. The illusion of preservation: a global environmental argument for the local production of natural resources. *J. Biogeogr.* 29, 1557–1568.
- Buckley, R., Zhong, L., Ma, X., 2017. Visitors to protected areas in China. *Biol. Conserv.* 209, 83–88.
- Clark, J.S., Bell, D.M., Hersh, M.H., Nichols, L., 2011. Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Glob. Chang. Biol.* 17, 1834–1849.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Hansen, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67, 534–545.
- Dixon, R.K., Brown, S., Houghton, R.E.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–189.
- Doxa, A., Albert, C.H., Leriche, A., Saatkamp, A., 2017. Prioritizing conservation areas for coastal plant diversity under increasing urbanization. *J. Environ. Manag.* 201, 425–434.
- Dudley, N. (Ed.), 2008. Guidelines for Applying Protected Area Management Categories. IUCN, Gland, Switzerland.
- Dudley, N., Parrish, J.D., Redford, K.H., Stolton, S., 2010. The revised IUCN protected area management categories: the debate and ways forward. *Oryx* 44, 485–490.
- Etter, A., McAlpine, C.A., Seabrook, L., Wilson, K.A., 2011. Incorporating temporality and biophysical vulnerability to quantify the human spatial footprint on ecosystems. *Biol. Conserv.* 144, 1585–1594.
- Feeley, K.J., Silman, M.R., 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. *Glob. Chang. Biol.* 16, 1830–1836.
- Fernández-Martínez, M., Vicca, S., Janssens, I.A., Campioli, M., Peñuelas, J., 2016. Nutrient availability and climate as the main determinants of the ratio of biomass to NPP in woody and non-woody forest compartments. *Trees* 30, 775–783.
- Foxcroft, L.C., Rouget, M., Richardson, D.M., 2007. Risk assessment of riparian plant invasions into protected areas. *Conserv. Biol.* 21, 412–421.
- Gagné, S.A., Eigenbrod, F., Bert, D.G., Cunningham, G.M., Olson, L.T., Smith, A.C., Fahrig, L., 2015. A simple landscape design framework for biodiversity conservation. *Landscape Urban Plan.* 136, 13–27.
- Gilliam, F.S., 2016. Forest ecosystems of temperate climatic regions: from ancient use to climate change. *New Phytol.* 212, 871–887.
- Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., Wang, C., 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* 11, 1395–1411.
- Hannah, L., 2008. Protected areas and climate change. *Ann. N. Y. Acad. Sci.* 1134, 201–212.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Biol. Lett.* 8, 23–29.
- IUCN, 1994. Guidelines for Protected Area Management Categories. CNPPA with the assistance of WCMC, Cambridge, UK.
- Jenkins, C.N., Joppa, L., 2009. Expansion of the global terrestrial protected area system. *Biol. Conserv.* 142, 2166–2174.
- Jones, K.R., Watson, J.E., Possingham, H.P., Klein, C.J., 2016. Incorporating climate change into spatial conservation prioritisation: A review. *Biol. Conserv.* 194, 121–130.
- Joppa, L.N., Loarie, S.R., Pimm, S.L., 2009. On population growth near protected areas. *PLoS One* 4, e2479.
- Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.* 21 (4), 393–404.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H., Barthlott, W., 2005a. Global patterns of plant diversity and floristic knowledge. *J. Biogeogr.* 32, 1107–1116.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H., Barthlott, W., 2005b. Global patterns of plant diversity and floristic knowledge. *J. Biogeogr.* 32, 1107–1116.
- Leroux, S.J., Krawchuk, M.A., Schmiegelow, F., Cumming, S.G., Liso, K., Anderson, L.G., Petkova, M., 2010. Global protected areas and IUCN designations: Do the categories



- match the conditions? *Biol. Conserv.* 143, 609–616.
- Leu, M., Hanser, S.E., Knick, S.T., 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecol. Appl.* 18, 1119–1139.
- Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol. Conserv.* 131, 433–445.
- Locke, H., Dearden, P., 2005. Rethinking protected area categories and the new paradigm. *Environ. Conserv.* 32, 1–10.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243.
- Mawdsley, J.R., O' Malley, R., Ojima, D.S., 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conserv. Biol.* 23, 1080–1089.
- Maxted, N., Dulloo, E., V Ford-Lloyd, B., Iriondo, J.M., Jarvis, A., 2008. Gap analysis: a tool for complementary genetic conservation assessment. *Divers. Distrib.* 14, 1018–1030.
- McConnachie, M.M., Wilgen, B.W., Richardson, D.M., Ferraro, P.J., Forsyth, A.T., 2015. Estimating the effect of plantations on pine invasions in protected areas: a case study from South Africa. *J. Appl. Ecol.* 52, 110–118.
- McKinney, M.L., 2002. Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. *Divers. Distrib.* 8, 311–318.
- McShane, T.O., Hirsch, P.D., Trung, T.C., Songorwa, A.N., Kinzig, A., Monteferrri, B., Mutekanga, D., Thang, H.V., Dammert, J.L., Pulgar-Vidal, M., Welch-Devine, M., Peter Brosius, J., Coppolillo, P., O'ÁConnor, S., 2011. Hard choices: making trade-offs between biodiversity conservation and human well-being. *Biol. Conserv.* 144, 966–972.
- Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S., Wilmsking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J., Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jørgensen, R.H., Buchwal, A., Buras, A., Naito, A.T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015. Climate sensitivity of shrub growth across the tundra biome. *Nat. Clim. Chang.* 5, 887.
- Olson, D.M., Dinerstein, E., 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv. Biol.* 12, 502–515.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Loucks, C.J., 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* 51, 933–938.
- Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akcakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffman, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B., Rondinini, C., 2015. Assessing species vulnerability to climate change. *Nat. Clim. Chang.* 5, 215–224.
- Pan, Y.D., Birdsey, R.A., Fang, J.Y., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S.L., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993.
- Pauchard, A., Alaback, P.B., 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. *Conserv. Biol.* 18, 238–248.
- Porter, E.M., Bowman, W.D., Clark, C.M., Compton, J.E., Pardo, L.H., Soong, J.L., 2013. Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity. *Biogeochemistry* 114, 93–120.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. *Bioscience* 52, 891–904.
- Shaver, G.R., Billings, W.D., Chapin, F.S., Giblin, A.E., Nadelhoffer, K.J., Oechel, W.C., Rastetter, E.B., 1992. Global change and the carbon balance of arctic ecosystems. *Bioscience* 42, 433–441.
- Speranza, C.I., Kiteme, B., Ambenje, P., Wiesmann, U., Makali, S., 2010. Indigenous knowledge related to climate variability and change: insights from droughts in semi-arid areas of former Makuani District, Kenya. *Clim. Chang.* 100, 295–315.
- Su, S., Ma, X., Xiao, R., 2014. Agricultural landscape pattern changes in response to urbanization at ecoregional scale. *Ecol. Indic.* 40, 10–18.
- Svenning, J.C., Eiserhardt, W.L., Normand, S., Ordóñez, A., Sandel, B., 2015. The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annu. Rev. Ecol. Evol. S.* 46, 551–572.
- Thuiller, W., Broennimann, O., Hughes, G., Jrm, A., Midgley, G.F., Corsi, F., 2010. Vulnerability of african mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob. Chang. Biol.* 12, 424–440.
- Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H.M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H.P., Rondinini, C., Smith, R.J., Venter, M., Watson, J.E.M., 2014. Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* 12, e1001891.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7, 12558.
- Venter, O., Magrath, A., Outram, N., Klein, C.J., Marco, M.D., Watson, J.E., 2017. Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. *Conserv. Biol.* 32, 127–134.
- Wade, T., Riitters, K., Wickham, J., Jones, K.B., 2003. Distribution and causes of global forest fragmentation. *Conserv. Ecol.* 7, 7.
- Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T., Gittleman, J.L., 2013. Targeting global conservation funding to limit immediate biodiversity declines. *Proc. Natl. Acad. Sci. USA* 110, 12144–12148.
- Wan, J.Z., Wang, C.J., Qu, H., Liu, R., Zhang, Z.X., 2018. Vulnerability of forest vegetation to anthropogenic climate change in China. *Sci. Total Environ.* 621, 1633–1641.
- Watson, J.E., Iwamura, T., Butt, N., 2013. Mapping vulnerability and conservation adaptation strategies under climate change. *Nat. Clim. Chang.* 3, 989.
- Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. *Nature* 515, 67–73.
- Weigelt, P., Steinbauer, M.J., Cabral, J.S., Kreft, H., 2016. Late Quaternary climate change shapes island biodiversity. *Nature* 532, 99.
- Williams, J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci. USA* 104, 5738–5742.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., Brashares, J.S., 2008. Accelerated human population growth at protected area edges. *Science* 321, 123–126.
- Wood, C.L., McInturf, A., Young, H.S., Kim, D., Lafferty, K.D., 2017. Human infectious disease burdens decrease with urbanization but not with biodiversity. *Phil. Trans. R. Soc. B* 372, 20160122.
- Woolmer, G., Trombulak, S.C., Ray, J.C., Doran, P.J., Anderson, M.G., Baldwin, R.F., Morgan, A., Sanderson, E.W., 2008. Rescaling the human footprint: a tool for conservation planning at an ecoregional scale. *Landscape Urban Plan.* 87, 42–53.
- Yuan, Q., Wu, S., Dai, E., Zhao, D., Ren, P., Zhang, X., 2017. NPP vulnerability of the potential vegetation of China to climate change in the past and future. *J. Geogr. Sci.* 27, 131–142.